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CROWN-OF-THORNS STARFISH OUTBREAKS ON THE GREAT BARRIER REEF: A GEOLOGICAL PERSPECTIVE BASED UPON THE SEDIMENT RECORD.

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Abstract

Over the last 30 years the crown-of-thorns starfish (_Acanthaster planci_) has caused extensive damage to many reefs in the Great Barrier Reef Province. Surface sediment of two such reefs, John Brewer Reef and Green Island Reef, is greatly enhanced in _A. planci_ skeletal elements relative to the element abundance in the surface sediment of Heron Island Reef which, during the same 30 years, maintained very low-density starfish populations. Carbon-14 accelerator mass spectrometry (AMS) dating indicates that skeletal elements from the surface sediment of John Brewer and Green Island Reefs are of contemporary age. Core sampling shows that subsurface sediment at John Brewer and Green Island Reefs contains _A. planci_ element densities comparable to those found in the surface sediment at these localities. Physical and biological reworking of elements within the sediment precludes the recognition of individual outbreaks in core stratigraphy. AMS element dates and conventional bulk sediment dates show that subsurface elements are generally prehistoric and conform to an age structure preserved in the sediment pile. The density and distribution of subsurface elements suggest that _A. planci_ outbreaks are not a recent phenomenon, but have been an integral part of the ecosystem for at least 7000 years on John Brewer Reef and 3000 years on Green Island Reef.

Introduction

The crown-of-thorns starfish (Acanthaster planci L.) has been responsible for the widespread destruction of scleractinian corals on many reefs in the Indo-Pacific region over the last 30 years. Coral devastation directly attributable to A. planci predation has occurred in areas as widespread as Micronesia (Chesher 1969; Marsh and Tsuda 1973), southern Japan (Nishihira and Yamazato 1974; Yamaguchi 1987), Polynesia (Devaney and Randall 1973) and Australia's Great Barrier Reef (GBR) (Endean and Stablum 1973; Pearson 1981; Done 1985).

Two distinct outbreaks have been recorded on the GBR since 1962. On both occasions, the outbreaks were observed first on Green Island Reef (Fig. 1) apparently having originated on reefs immediately to the north (see Moran 1986). Following the initiation of each outbreak, reefs to the south have been progressively affected. To date, the majority of A. planci outbreaks have been reported between Princess Charlotte Bay (14°15'S) and Bowen (20°01'S) (Moran 1987; Fig 1). Isolated outbreaks have also been recorded in the Swain Reefs Complex, north-east of Gladstone (Pearson and Garrett 1978; Endean and Cameron 1985; Great Barrier Reef Marine Park Authority (GBRMPA) unpublished data base; Fig. 1).

Results from recent surveys (COT-CCEP Crown-of-thorns Study 1986-7) reveal considerable spatial variation in the magnitude of outbreaks. The central third of the GBR has sustained most damage with 35% of reefs seriously affected and 30% affected to a lesser degree (Moran 1987).

Much of the current debate centres on the time-span over which these outbreaks have occurred. Some commentators (Endean and Stablum 1975; Cameron and Endean 1981; Endean and Cameron 1985) regard the massive coral damage in the GBR as a recent phenomenon, directly attributable to the activities of man following European settlement of the north Queensland coast. Conversely, outbreaks may be long-standing and an integral part of the ecological framework under which the GBR has developed (Potts 1981).

Assessment of the sediment record offers a potential means of examining past patterns of A. planci activity on the GBR. A basic methodology for such a study was established by Frankel (1977, 1978). A. planci contains an intricate mesodermal skeleton of calcite elements which are released on death or predation and subsequent tissue decay and which should accumulate as inert grains in the reefal sediment record. Frankel (op. cit.) attempted to assess the late Holocene fossil record of A. planci in the GBR but his data have been criticised as too small to sustain his conclusions (Moran et al. 1986).

Our study was based on the following approach :

1. Extensive sampling of surface sediment from selected reefs to evaluate the relationship between extremes in contemporary population densities and the contribution of A. planci skeletal elements to contemporary sediment;
2. Sampling of subsurface sediment cored from reefs known to have experienced massive population outbreaks of A. planci predation in the last 30 years;
3. Analysis of cored sediment for A. planci elements and assessment, by carbon-14 dating techniques, of the age structure preserved

within the cores;

4. Recognition of signatures of A. planci skeletal element density in ancient sediment of known age on the basis of an established contemporary relationship.

Methods

Reef selection

Three reefs were selected for surfacial sediment sampling (Fig. 1) based on their well-documented recent histories of A. planci population levels. John Brewer Reef and Green Island Reef have both experienced two devastating outbreaks since 1962. Heron Island Reef has maintained a low-density population of A. planci during this period and was used as the control in this study.

An outbreak of A. planci occurred on Green Island Reef between 1962 and 1967 (Endean 1969). A second population increase was recorded in 1979 and by 1980 the population was estimated to comprise 2 million starfish (Kenchington and Pearson 1981). Estimates of coral mortality exceeded 90% (Endean and Cameron 1985). A. planci was again rare by 1983 (Bradbury et al. 1985).

The first outbreak on John Brewer Reef occurred between 1969 and 1971 (Endean and Stablum 1973) and caused almost total destruction of the living coral (Pearson 1981). The effects of the second outbreak, which commenced in May 1983, were at least as extensive as the first (Done 1985). By October 1984, starfish numbers on John Brewer Reef had declined markedly (Moran et al. 1985) and they are now scarce (Moran pers. comm.).

There are no records of A. planci aggregations on Heron Island

Reef (GBRMPA unpublished data base) which has been adequately monitored since 1956 when a permanently manned research station was established (Hill 1985).

John Brewer and Green Island Reefs were selected for subsurface sampling because of their susceptibility to A. planci predation over the last 30 years. If such predation is a recurrent pattern, these reefs should also contain A. planci skeletal elements within their ancient sediment bodies.

Surface sediment sampling and processing

Surface sediment samples (3-4 kg) were collected by a jawed grab sampler capable of retrieving approximately 3200 cm^3 of sediment to a maximum depth of about 4 cm at a time. In shallow areas ($\leq$10 m), where the coarseness of the sediment rendered the grab sampler ineffective, samples were collected by divers using SCUBA. John Brewer Reef was the first reef investigated with surface sampling down to 39 m water depth. In view of the enhanced recovery of A. planci skeletal elements for this reef at $\leq$20 m water depth (Fig. 2a), the surface sampling programs for Green Island and Heron Island Reefs were modified accordingly. Fifty eight surface samples were collected on John Brewer Reef in September, 1985 (Fig. 2a), 46 on Green Island Reef in January, 1986 (Fig. 2b) and 55 on Heron Island Reef in May, 1986 (Fig. 2c).

Samples were washed in dilute sodium hypochlorite to remove organic coatings, soaked twice in tap water to remove salt, dried and subdivided. One kilogram samples, dry sieved at 0.5-1.0, 1.0-2.0, 2.0-4.0, and $\geq$4.0 mm size intervals, were picked for A. planci skeletal elements under a binocular microscope.

Subsurface sediment sampling and processing

A pontoon-supported vibracorer was used for subsurface coring of sediment in shallow water. The leeward slope of John Brewer Reef was cored with a ship-deployed vibracorer. Sediment cores were collected in 76 mm I.D. aluminium piping measuring 5.8 and 4.5 m in length for the respective vibracorers. Finger core-catchers prevented sediment loss from the piping during core retrieval.

High frequency seismic profiles were utilised to survey sediment bodies on the leeward slope of John Brewer Reef to identify sites suitable for coring. All other sites were in sufficiently shallow water for visual assessment. The absence of substantial sediment bodies rendered the windward slopes unsuitable for coring.

Seven sites, selected to cover a range of depositional environments, were cored on John Brewer Reef: three from the lagoon, one from an indentation in the leeward rim (the "Notch") and three from different depths on the leeward slope (Fig. 3a). Four to six cores were recovered from each site. Four replicate cores from site 11, three from site 12 and two cores from each of the five other sites were selected for picking on the basis of core recovery length. Four sites on the leeward shoal and two on the reef flat of Green Island Reef were selected by visual inspection for coring (Fig. 3b). Two replicate cores from each site were picked.

Each core was split longitudinally. One half was subdivided into 250 g intervals, representing an average core length of 8-10 cm. These were soaked 3 times in tap water, dried and sieved to the same size fractions as the surface samples.

Variability in compaction between replicate cores and uncertainty as to how sediment behaves during the vibracoring process make accurate recalibration impossible. Recalculation of core recovery to penetration length (Figs 4, 5) assumes uniform sediment compaction throughout the core permitting a more direct comparison of element distribution between replicate cores than would be the case had no correction been taken into account. Future references to core ane interval lengths are based on penetration data.

Element identification

A detailed examination of the morphology and ultrastructure of *A. planci* skeletal elements (Walbran 1987) demonstrated that they are readily distinguished from the elements of other asteroids common on the GBR. Whilst *A. planci* elements are morphologically distinct, it is their colour, which ranges from a light mauve through to dark purple and, at times, an intense orange-red, that facilitates initial identification in a tray of mixed reefal sediment. A combination of colour, morphological features and a distinctive surface texture, reflecting detail of the stereom structure, permits the unequivocal recognition of *A. planci* elements under a binocular microscope.

Carbon-14 dating

Liquid scintillation counting (LSC) of bulk (50 g minimum weight) surface and core sediment samples was undertaken at the Radiocarbon

Dating Laboratory, Australian National University (ANU), Canberra. Dating of individual and grouped A. planci elements (10-15 mg minimum weight) from within sampled intervals was carried out on the accelerator mass spectrometry (AMS) facilities of the Institute of Nuclear Sciences (INS), Department of Scientific and Industrial Research, Lower Hutt, New Zealand. Procedures followed at ANU are set out in Gupta and Polach (1985) and those at INS in Sparks et al. (1986), Lowe and Judd (1987) and Wallace et al. (1987).

Fifty four bulk sediment samples, selected from the John Brewer and Green Island Reef core sets to provide down-core age control within each depositional environment, were dated by LSC. Sixteen skeletal element samples, submitted in two batches, were dated by AMS. The minimum sample weight of 10 mg for the first 10-sample batch proved to be insufficient, resulting in a low yield of graphite (D. Lowe pers. comm.) and gaving rise to large dating errors. An increase in minimum weight to 15 mg for the second batch of 10 samples produced smaller errors. In addition, two bulk surface samples and the corresponding A. planci material from each of the two reefs were dated. AMS samples were washed in an ultrasonic bath for 30 minutes prior to submission. Minor amounts of secondary carbonate coating could not be removed. Scanning electron microscopy revealed these coatings to be thin surficial encrustations and volumetrically insignificant.

Dates presented in the text of this paper are the real or reservoir-corrected ages determined by subtracting the Gillespie-Polach factor of 450 ± 35 years (Gillespie and Polach 1979) from the dates reported by the carbon-14 laboratories and designated as years

BP*. Laboratory-reported conventional ages as well as real ages are given in the tables.

Statistical analysis

The Mann-Whitney U-test for non-parametric data was used to assess inter-reef variability in element recovery from surficial sediment of the three reefs and to compare element abundance, per sampled interval, from above and below below 200 cm core depth for the John Brewer and Green Island Reef core suites. The Kolmogorov-Smirnov 'two-sample' test assesses the comparability of two sample sets and was used to compare replicate cores in terms of element contents.

Results

Element Recovery

Surface Sediment

A total of 663 elements were recovered from the 59 surface sample sites on John Brewer Reef (Fig. 2a), an average of 11.2 (s.d. 21.5) elements per 1 kg sample. The windward slope 10 m and leeward slope 10 m environments were the most productive with maxima of 93 and 21 elements per sample respectively. With the apparent exception of the base of patch reefs, the lagoon was devoid of elements in the surface sediment. The vast majority of elements were recovered from water depths of 20 m or less. If results for depths of ≤20 m only are considered, the number of sample sites on John Brewer Reef is reduced to 38 and element recovery to 649, but average recovery per 1 kg sample increases to 17.1 (s.d. 24.9).

The 46 surface sample sites on Green Island Reef produced 997

A. planci elements (Fig. 2b), an average of 21.7 (s.d. 23.5) per 1 kg sample. No obvious pattern of element distribution is apparent with the exception of the reef flat where the abundance is reduced. Green Island Reef lacks the well-defined rim and lagoon of John Brewer Reef. The somewhat erratic distribution of elements it displays may reflect this poor morphological differentiation.

Extensive sampling on Heron Island Reef produced only two elements from the 55 surface samples processed, each from markedly distinct environments (Fig. 2c).

Element recovery from surface sediment of John Brewer and Green Island Reefs was significantly greater than that for Heron Island Reef ($\underline{P}<0.001$, Mann-Whitney _U_-test; Table 1). The difference in element recovery between John Brewer ($\leq$20 m) and Green Island Reefs was also significant ($\underline{P}=0.024$; Table 1).

Subsurface Sediment

Cores recovered from John Brewer Reef ranged in length from 271 to 501 cm (Fig. 4). Element distribution in the subsurface is discontinuous and subject to fluctuation (Fig. 4). Lagoon and "Notch" environments (Fig. 3a, sites 6, 7 and 8) contained the most elements (x = 1.9/250 g sample), but recovery from leeward slope environments at 25 and 39 m water depth (Fig. 3a, sites 12 and 13) was also substantial (x = 1.3/250 g sample). Maximum element content for individual sample intervals was 10 from cores JB8a (454.5-466.0 cm) and JB8b (354.0-365.0 cm).

Core recovery on Green Island Reef ranged from 454 and 541 cm (Fig. 5). As was the case with surface sediment, element recovery in the subsurface of Green Island Reef was substantially greater than that for John Brewer Reef. Element distribution is continuous in most cores, although subject to fluctuation (Fig. 5). Site 6 contained the greatest abundance and highest concentration of elements with a maximum of 17 recovered from a single sampled interval (GI6b 454.0-469.0 cm).

Visual inspection of both core sets suggests element abundance increases below 200 cm core depth. This is borne out by statistical analysis which shows that element abundance per sample interval is significantly greater ($\underline{P}<0.001$, Mann-Whitney $\underline{U}$-test) below 200 cm core depth than above for John Brewer and Green Island Reefs (Table 2). Results of the Kolmogorov-Smirnov analysis (Table 3) indicate that, with the exception of site 13 on John Brewer Reef, where the maximum frequency difference exceeds the critical value, sample suites from replicate cores reflect a common population and suggest that data for individual cores reasonably reflect the distributional pattern of elements within the sediment bodies as a whole.

Carbon-14 Dating

LSC dates reveal the preservation of an age structure in the subsurface sediment of John Brewer and Green Island Reefs (Fig. 6; Table 4). Only two cases of age reversal (JB12a 199.5 cm and GI6b 209.0-219.0 cm) are represented in the bulk sediment age suites. Surface sediment ages for bulk samples (Table 5) ranged from Modern (dated within the last 200 years) to 250 ± 70 years BP* with corresponding grouped elements giving Modern or >Modern (post AD1954 when the initiation of atmospheric nuclear testing atmospheric testing disrupted the natural radiocarbon system) dates. A broad correlation is displayed between the bulk sediment and element dates for corresponding intervals (Fig. 6) although this is, in part, a function of large errors in the AMS results (Table 6), particularly in respect to the first (10 mg minimum weight) batch. A closer age correlation is evident between the second (15 mg minimum weight) batch of skeletal material and corresponding bulk sediment. Age disparities in the subsurface results range to at least 1000 years and possibly as much as 1600 years if the Modern age for GI6b (454.0-469.0 cm) is accepted. An age disparity also applies to the surface sediment at site JB39 (Fig. 2a) where the bulk sediment gave an age of 250 ± 70 years BP* and the AMS age for A. planci elements returned a Modern age (Table 5).

Discussion

Surface Sediment

The abundance of A. planci elements in the surface sediment of John Brewer and Green Island Reefs contrasts markedly with their almost total absence from Heron Island Reef. Although data were collected from only three reefs, they are the only reefs in the GBR for which the activity of A. planci has been adequately monitored over the last three decades. In addition, they represent population extremes for A. planci; episodically very high (John Brewer and Green Island Reefs) and consistently very low (Heron Island Reef).

Reports from the Red Sea (Ormond et al. 1973; Ormond and Campbell 1974) and Western Australia (Wilson and Marsh 1974) suggest that A. planci may aggregate from low-density populations as a part of their normal feeding and/or breeding behaviour. Potentially misleading results may, therefore, come from limited sampling of reefs (see Moran et al. 1986), especially when compounded by poor data on contemporary A. planci activity. We therefore extensively sampled the surface sediment of each reef.

For John Brewer Reef in particular, the density of A. planci elements in the surface sediment closely correlates with zones of active coral growth. Element density was highest in areas adjacent to the reef rim, especially the windward rim, where coral cover is enhanced and decidedly lower in samples from the lagoon and leeward slope sediment apron (Fig. 2a). This observation is consistant with the results of Moran et al. (1985) who found the highest concentrations of live A. planci on the windward slope. A similar pattern of element distribution exists at Green Island Reef but is less well-defined due to the poor morphological differentiation of this reef. Radiocarbon dating confirms that surface elements from John Brewer and Green Island Reefs are Modern or ≥Modern in age. The contribution of A. planci skeletal elements to the surface sediment therefore appears to reflect the distribution of the animals during outbreaks.

Mortality patterns for A. planci are poorly known. The absence of a documented mass mortality of starfish, the appearance of adult starfish at depth on reefs prior to the initiation of an outbreak phase and reports of individuals from inter-reef areas have been cited as evidence for starfish migration to adjacent reefs following an outbreak (Endean 1973, 1977; Endean and Stablum 1973). Other evidence, however, indicates that most starfish die on the reef rather than migrate. In individuals from high-density *A. planci* populations on Helix Reef, central GBR, gonad development continued at the expense of the body wall and pyloric caecae during post-juvenile growth (Kettle and Lucas 1987). For many *A. planci*, tissue-wasting terminates in death of the animal on the reef which hosted the outbreak. There is no evidence that any part of the population migrated from Helix Reef following the outbreak (Kettle pers. comm.). Studies of juvenile *A. planci* on Suva Reef, Fiji, also support the view that outbreaks do not result from the migration of starfish between reefs (Zann et al. 1987).

Subsurface Sediment

A. planci elements are less common in the subsurface sediment of John Brewer Reef compared to that of Green Island Reef. This may largely be a function of the availability of suitable vibracoring sites on John Brewer Reef which are, as a consequence of local bathymetry and substrate, restricted to lagoonal and leeward slope environments.

Core results indicate a more uniform geographic distribution of elements than that displayed in the surface sediment (Figs 4; 5). This is especially apparent for John Brewer Reef where element recovery was more consistant in the subsurface relative to surface sediment for samples representing both lagoonal and leeward slope environments. We ascribe this to the reworking and dispersal of elements prior to their internment in the sediment body, as indicated by the generally poorer preservational state of subsurface elements. Grains in the upper few centimetres of sediment, including A. planci elements derived from contemporary outbreaks, are subjected to similar abrasion and dispersal prior to final burial.

In addition to problems arising from physical reworking, the detailed interpretation of element distribution within the cores is complicated by substantial biological reworking of the sediment pile. The dominant agents of bioturbation in tropical reef environments are callianassid shrimps. These burrowers recycle vast quantities of sediment during feeding (Roberts et al. 1981; de Vaugelas and de Saint-Laurent 1984; de Vaugelas et al. 1986). Although Callianassa burrows in excess of 2 m depth have been reported from Eniwetok Atoll in the Marshall Islands (Suchanek et al. 1986), the active reworking of finer-grained sediment ($\leq$1-2 mm) by Callianassa in reef lagoons of the GBR is restricted to the top 60 cm of the sediment pile (Tudhope and Scoffin 1984). Coarser material is stored in deeper chambers.

The storage of coarse and recycling of finer particles by Callianassa has important implications for this study. More than 82% of A. planci elements recovered from the subsurface are in the 0.5-1.0 mm size fraction and only 0.6% are $\geq$2 mm in size. The vast majority of contemporary elements will therefore be retained within the zone of callianassid activity.

The down-core distribution of elements is a legacy of physical and biological reworking. This, combined with overall sedimentation rates in the order of 1-3 m per thousand years, negates any prospect that short-term periodic events, such as individual A. planci outbreaks, will be preserved as a recognisable signature in the sedimentary record. It is noteworthy that element concentration in the uppermost interval of all cores is no greater than that of underlying intervals. Contemporary outbreaks are therefore not recognisable in the sedimentary record as a unique layer discriminated by abnormally high quantities of A. planci elements.

Our conclusions in this regard conflict with those of Frankel (1977, 1978) who obtained small numbers of elements from reconnaissance airlift bore hole sampling of subsurface sediment on 22 individual reefs of the GBR, including Green Island Reef. Frankel's data indicated that elements were restricted to sporadic horizons in ancient sediment bodies which he thaught likely to reflect past outbreak cycles at 250-300 year intervals. Our results from Green Island Reef cores, with a much larger number of elements recovered per unit weight of sediment and a more uniform down-core distribution, do not support this contention.

The possibility that all A. planci elements in the cores represent biological reworking of contemporary material into the sediment pile can be eliminated on two grounds. Firstly, A. planci elements are present within cores at depths of greater than 2 m, well beyond the range of contemporary Callianassa activity. Secondly, dating of individual and grouped elements obtained from the subsurface have, with one exception, given old ages.

Reworking has doubtless impaired the age structure preserved in the cores, especially those from shallower sites, but our dating results indicate that it has not been destroyed. A close relationship between core depth and bulk sediment age is apparent in all cores for which we have age data. Correlation between core depth and bulk sediment age is especially close for core JB13a (r^2 = 0.994) which was taken in a water depth of 39 m. *Callianassa* activity is limited to about 20 m maximum water depth on nearby Davies Reef (Tudhope and Scoffin 1984) and the sediment record at site 13 may have escaped significant bioturbation.

Disparities in the ages of individual and grouped elements and the bulk sediment intervals from which they were recovered show that the stratigraphic integrity of individual grains within the sediment pile has been disturbed. Bioturbation, which clearly influences contemporary sedimentation, is the most likely cause of major disruption. The distribution of *A. planci* elements within the sediment body is most unlikely to reflect the detailed temporal distribution of past populations.

The final question to be addressed is whether the core results demonstrate the presence of *A. planci* in outbreak proportions in prehistoric times. As we have discussed, the stratigraphy of sediment bodies in shallow-water reefal environments is not preserved in sufficient detail to permit the identification of short-term periodic events. The stratigraphic record of *A. planci* elements is time-averaged and shows only coarse trends. Knowledge of contemporary sedimentary processes indicates that *A. planci* elements derived from contemporary outbreaks on John Brewer and Green Island Reefs will become dispersed in the sedimentary record as it accumulates. The down-core distribution of *A. planci* elements documented here is consistent with a long period, at least 7000 years on John Brewer Reef and 3000 years on Green Island Reef, of repeated *A. planci* outbreak cycles, the skeletal record of which has become dispersed in the sedimentary record. Further, the enhanced element abundance apparent below 200 cm core depth and the well preserved sediment record at site 13 on John Brewer Reef suggest a decrease in the prevalence of A. planci on these reefs over the last 1000-2000 years.

Present and past distributional patterns of A. planci elements in the sediment are consistent with the view that recurrent population outbreaks typify A. planci behaviour. Any alternative hypothesis requires a long-term, stable, "intermediate level" A. planci population density on the two reefs in question which coincidentally has resulted in an element distribution in ancient sediment matching that now found at the surface and clearly related to contemporary outbreak cycles.

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Fig. 1. Location of reefs sampled within the Great Barrier Reef (GBR).

Fig. 2. Number of *A. planci* elements recovered from surfacial sediment sampling sites on John Brewer Reef, Green Island Reef and Heron Island Reef. No elements were recovered from unnumbered sites. Numbers bracketed identify surface sample sites from which bulk sediment and grouped element ages were obtained. Dashed lines delineate environmental boundaries.

Fig. 3. Vibracore sites (numbered) on John Brewer Reef and Green Island Reef. Dashed lined delineate environmental boundaries.

Fig. 4. Subsurface *A. planci* element recovery from replicate cores, John Brewer Reef. Depositional environment and water depth are given. Bar scales show number of elements recovered from each core interval. Intervals sampled for Liquid Scintillation Counting (arrowed) and Accelerator Mass Spectrometry (shaded) are indicated. Real ages are shown for LSC-dated intervals.

Fig. 5. Subsurface *A. planci* element recovery from replicate cores, Green Island Reef. Depositional environment and water depth are given. Bar scales show number of elements recovered from each core interval. Intervals sampled for Liquid Scintillation Counting (arrowed) and Accelerator Mass Spectrometry (shaded) are indicated. Real ages are shown for LSC-dated intervals.

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Fig. 6. Subsurface age profiles for John Brewer and Green Island Reefs established by Liquid Scintillation Counting of bulk sediment samples and Accelerator Mass Spectrometry of *A. planci* skeletal elements.

Table 1. *Z* values and probabilities from Mann-Whitney *U*-tests for comparisons of *A. planci* element recovery from surface sediment samples on Heron Island Reef, John Brewer Reef and Green Island Reef.

Reefs	Number of Surface Samples	Number of Elements	$\bar{x} \pm$ s.d. of Elements per Sample	*Z*	*P*
Heron Island/John Brewer (all sites)	55/59	2/663	0.04 ± 0.19/11.2 ± 21.5	-6.40	<0.001
Heron Island/Green Island	55/46	2/997	0.04 ± 0.19/21.7 ± 23.5	-8.22	<0.001
John Brewer <20 m/Green Island	46/39	649/997	17.1 ± 24.9/21.7 ± 23.5	-2.25	0.024

Table 2. Z values and probabilities from Mann-Whitney U-tests for comparisons of *A. planci* element abundance per sample interval above and below 200 cm core depth in the John Brewer Reef and Green Island Reef core sets.

	Number of Core Intervals	Total Number of Elements	$\bar{x} \pm$ s.d. of Elements/ Interval	Z	P
John Brewer					
<200 cm	346	270	0.85 ± 0.59		
>200 cm	317	554	1.61 ± 1.00	-7.32	<0.001
Green Island					
<200 cm	231	490	2.21 ± 1.14		
>200 cm	360	1420	4.03 ± 1.53	-7.97	<0.001

Table 3. Maximum frequency differences and critical values from Kolmogorov-Smirnov tests comparing frequencies of *A. planci* elements in replicate core sets from John Brewer Reef and Green Island Reef.

	Number of Intervals per Core	Maximum Frequency Differences	Critical Values
John Brewer Cores			
1a & 1c	29 & 33	0.136	0.346
6a & 6b	42 & 48	0.104	0.287
7c & 7d	54 & 53	0.083	0.263
8a & 8b	54 & 48	0.111	0.269
11c & 11d	49 & 40	0.177	0.290
11c & 11e	49 & 47	0.059	0.278
11c & 11f	49 & 50	0.040	0.273
11d & 11e	40 & 47	0.148	0.293
11d & 11f	40 & 50	0.170	0.289
11e & 11f	47 & 50	0.076	0.276
12a & 12b	27 & 19	0.166	0.407
12a & 12c	27 & 18	0.093	0.414
12b & 12c	19 & 18	0.073	0.447
13a & 13b	34 & 25	0.500	0.359
Green Island Cores			
1b & 1c	48 & 53	0.148	0.272
2b & 2c	51 & 51	0.098	0.269
3a & 3b	55 & 53	0.136	0.262
4a & 4d	53 & 54	0.178	0.263
5b & 5c	51 & 50	0.170	0.271
6b & 6c	36 & 37	0.200	0.318

Table 4. Conventional and real ages of bulk sediment samples from John Brewer Reef and Green Island Reef core sets dated by Liquid Scintillation Counting. Core localities are given in Fig. 3.

Core Number/ Depositional Environment & Water Depth	Penetration Interval	Recovery Interval	ANU Reference Number	Conventional Age (± error)	Real Age (± error)
John Brewer Reef					
JB6c	0.0-2.5	0.0-2.0	ANU-5863	2630 ± 80	2180 ± 90
(Lagoon 8 m)	90.5-94.5	73.0-76.5	ANU-5864	2640 ± 80	2190 ± 90
	184.5-189.5	149.0-153.0	ANU-5865	2790 ± 80	2340 ± 90
	273.5-276.0	221.0-223.0	ANU-5866	3070 ± 80	2620 ± 90
	370.0-374.0	299.0-302.0	ANU-5867	3570 ± 80	3120 ± 90
	445.5-448.5	360.0-362.5	ANU-5868	4980 ± 80	4530 ± 90
JB7d	0.0-3.5	0.0-3.0	ANU-5870	2320 ± 80	1870 ± 90
(Lagoon 9 m)	91.5-94.5	75.0-77.5	ANU-5871	2390 ± 80	1940 ± 90
	182.5-185.5	150.0-152.5	ANU-5872	2650 ± 80	2200 ± 90
	274.0-277.0	225.0-227.5	ANU-5873	2930 ± 80	2480 ± 90
	365.5-368.5	300.0-302.5	ANU-5874	3530 ± 80	3080 ± 90
	441.0-444.0	362.0-364.5	ANU-5875	3840 ± 80	3390 ± 90
JB8b	0.0-4.0	0.0-3.0	ANU-5853	760 ± 70	310 ± 80
("Notch" 16 m)	54.0-66.0	42.0-51.0	ANU-5472	700 ± 60	250 ± 70
	146.0-156.0	113.0-121.0	ANU-5473	860 ± 60	410 ± 70
	237.5-242.5	184.0-188.0	ANU-5654	1130 ± 60	680 ± 70
	304.5-313.0	236.0-242.5	ANU-5655	1420 ± 70	970 ± 80
	324.5-334.0	251.5-259.0	ANU-5474	1780 ± 60	1330 ± 70
	405.0-413.0	314.0-320.0	ANU-5656	2760 ± 70	2310 ± 80
JB12a	0.0-5.0	0.0-3.0	ANU-5854	1930 ± 80	1480 ± 90
(Leeward slope 25 m)	66.5-71.5	40.0-43.0	ANU-5657	2040 ± 70	1590 ± 80
	133.0-136.0	80.0-82.0	ANU-5658	2000 ± 70	1550 ± 80
	166.0-171.0	100.0-103.0	ANU-5855	2770 ± 80	2320 ± 90
	199.5------	120.0------	ANU-5659	2310 ± 70	1860 ± 80
	246.0-252.5	148.0-152.0	ANU-5856	4950 ± 80	4500 ± 90
	289.0-294.0	174.0-177.0	ANU-5857	5530 ± 90	5080 ± 100
	320.5-328.0	193.0-197.5	ANU-5660	5770 ± 80	5320 ± 90

Table 4 continued.

JB13a 55.0-58.5	55.0-58.5	48.0-51.0	ANU-5670	2220 ± 70	1770 ± 80
(Leeward slope 39 m)	113.5-116.7	99.0-102.0	ANU-5671	3840 ± 80	3390 ± 90
	167.0-173.0	146.0-151.0	ANU-5672	4790 ± 80	4340 ± 90
	226.5-232.5	198.0-203.0	ANU-5673	6330 ± 80	5880 ± 90
	277.0-284.0	242.0-248.0	ANU-5674	8190 ± 90	7740 ± 100
Green Island Reef					
GI2c	89.5-92.0	75.0-77.0	ANU-5666	1860 ± 70	1410 ± 80
(Leeward shoal 6 m)	176.0-180.5	147.0-151.5	ANU-5667	2330 ± 70	1880 ± 80
	275.0-277.5	230.0-232.0	ANU-5668	2510 ± 70	2060 ± 80
	371.0-374.5	310.0-313.0	ANU-5669	2620 ± 70	2170 ± 80
	484.5-496.0	405.0-414.5	ANU-5475	2800 ± 70	2350 ± 80
GI5b	92.5-96.0	74.5-77.5	ANU-5661	1330 ± 70	880 ± 80
(Reef flat 1 m)	184.5-189.5	149.0-153.0	ANU-5662	2030 ± 70	1580 ± 80
	279.0-282.5	225.0-228.0	ANU-5663	2570 ± 70	2120 ± 80
	383.5-394.0	309.5-318.0	ANU-5645	2830 ± 70	2380 ± 80
	425.0-434.5	343.0-350.5	ANU-5476	3000 ± 70	2550 ± 80
	522.5-532.0	421.5-429.5	ANU-5477	3410 ± 70	2960 ± 80
GI6b	113.5-116.5	70.0-72.0	ANU-5664	820 ± 70	370 ± 80
(Leeward shoal 10 m)	209.0-219.0	129.0-135.0	ANU-5665	490 ± 60	40 ± 70
	210.5-219.0	130.0-135.0	ANU-5869	1030 ± 70	580 ± 80
	351.5-364.0	217.0-224.5	ANU-5478	1380 ± 70	930 ± 80
	423.0-439.0	261.0-271.0	ANU-5646	1820 ± 70	1370 ± 80
	439.0-454.0	271.0-280.0	ANU-5647	1910 ± 70	1460 ± 80
	454.0-469.0	280.0-289.5	ANU-5479	2030 ± 70	1580 ± 80
	469.0-489.5	289.5-302.0	ANU-5648	1950 ± 70	1500 ± 80
	505.0-520.5	312.0-321.0	ANU-5649	2000 ± 60	1550 ± 70
GI6c	357.0-369.5	251.5-260.0	ANU-5480	1720 ± 70	1270 ± 80
(Leeward shoal 10 m)	440.5-456.0	310.0-321.0	ANU-5481	2210 ± 70	1760 ± 80

Table 5. Conventional and real ages of bulk sediment samples dated by Liquid Scintillation Counting and grouped *A. planci* skeletal elements dated by Accelerator Mass Spectrometry from the same surfacial sites on John Brewer Reef and Green Island Reef. Sample localities are given in Figs 2a and 2b.

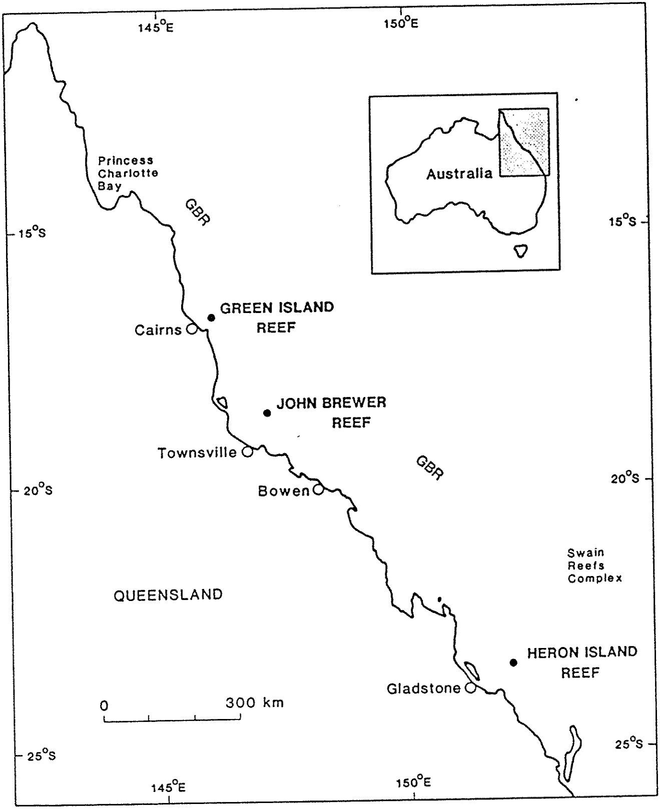
Bulk Sediment Details

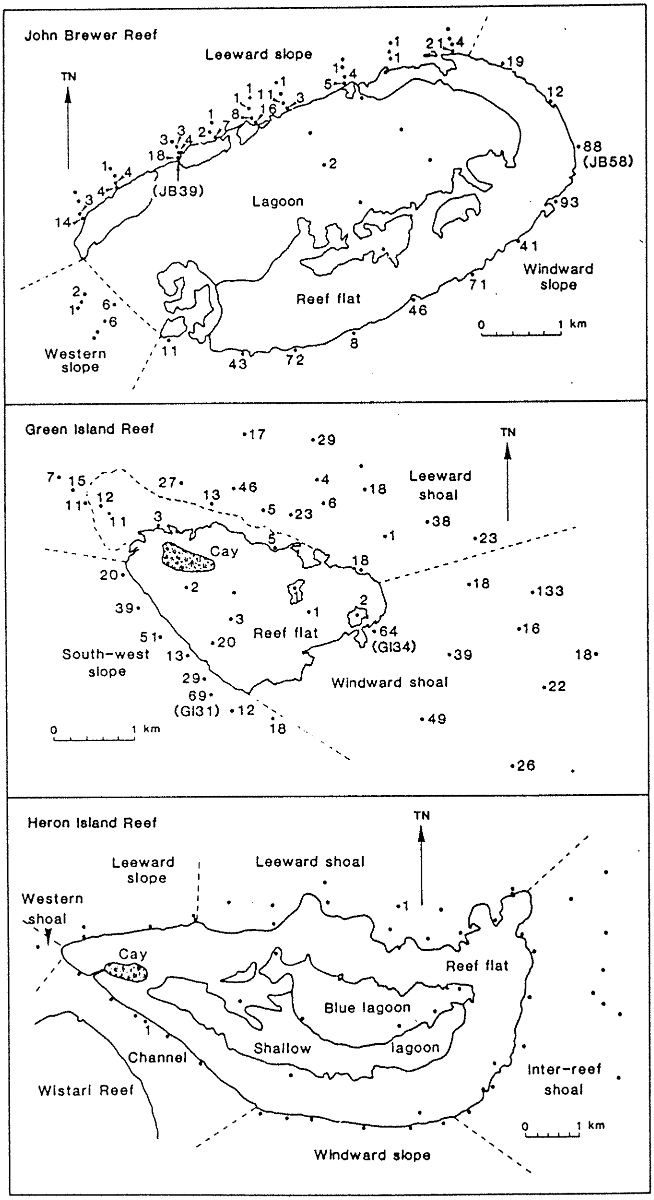
Sample Number	ANU Reference Number	Conventional Age (± error)/ %Modern	Real Age (± error)
John Brewer 39	ANU-5650	700 ± 60	250 ± 70
John Brewer 58	ANU-5651	98.5 ± 0.7 %M	Modern
Green Island 31	ANU-5652	290 ± 60	Modern
Green Island 34	ANU-5653	99.2 ± 0.7 %M	Modern

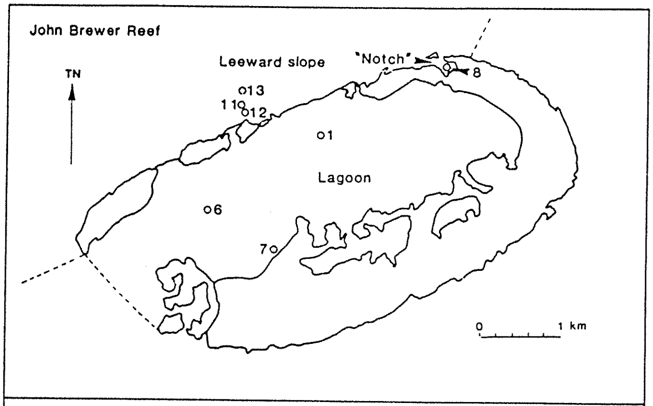
Skeletal Element Details

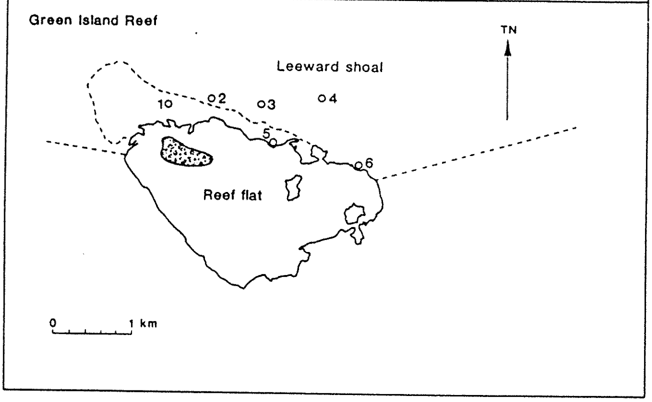
Sample Number	Number of Elements in Batch	Sample Weight (mg)[a]	% 2° Surface $CaCO_3$	Batch Number	Conventional Age %Modern	Real Age (± error)/
John Brewer 39	20	24.62	<3	2	111.1 ± 9.4 %M	>Modern
John Brewer 58	88	120.02	<5	2	111.3 ± 3.4 %M	>Modern
Green Island 31	68	121.08	<5	2	104.8 ± 4.3 %M	>Modern
Green Island 34	64	28.98	<3	2	344 ± 342	Modern

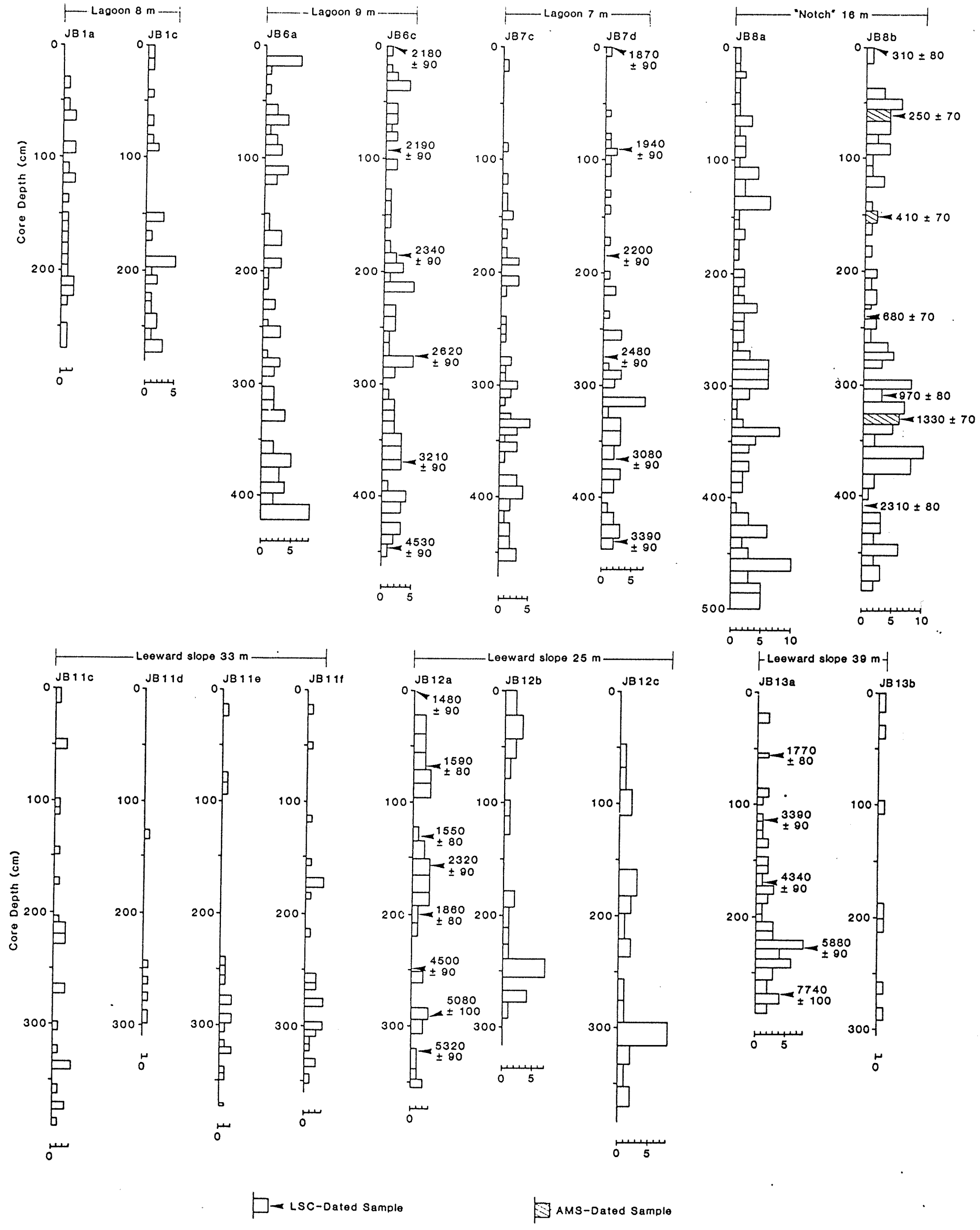
a - Weight as submitted to INS

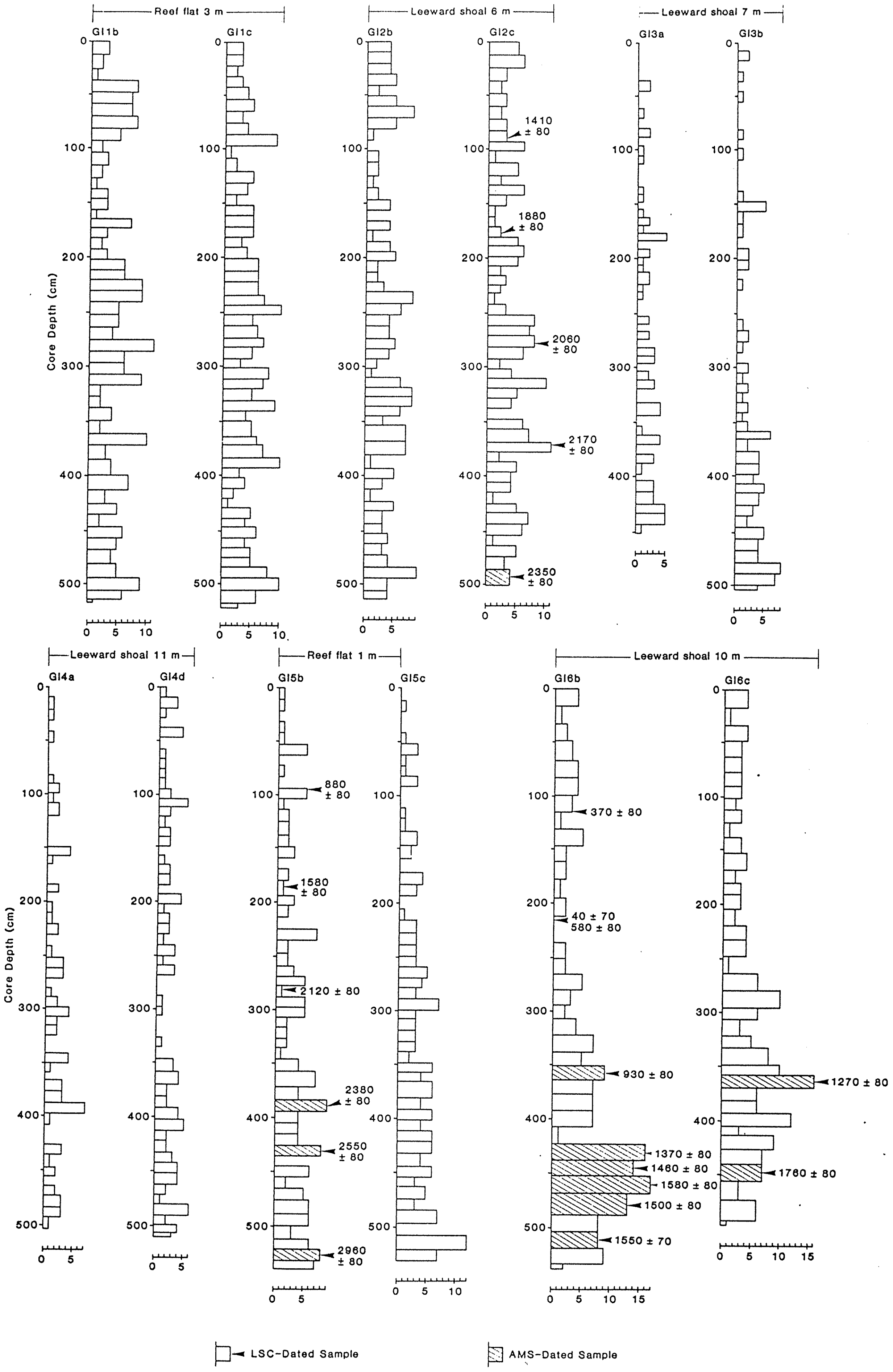

145°E
150°E
Princess
Charlotte
Bay
GBR
Australia
15°S
15°S
GREEN ISLAND
REEF
Cairns
JOHN BREWER
REEF
Townsville
GBR
Bowen
20°S
20°S
Swain
Reefs
Complex
QUEENSLAND
HERON ISLAND
REEF
Gladstone
0
300 km
25°S
25°S
145°E
150°E

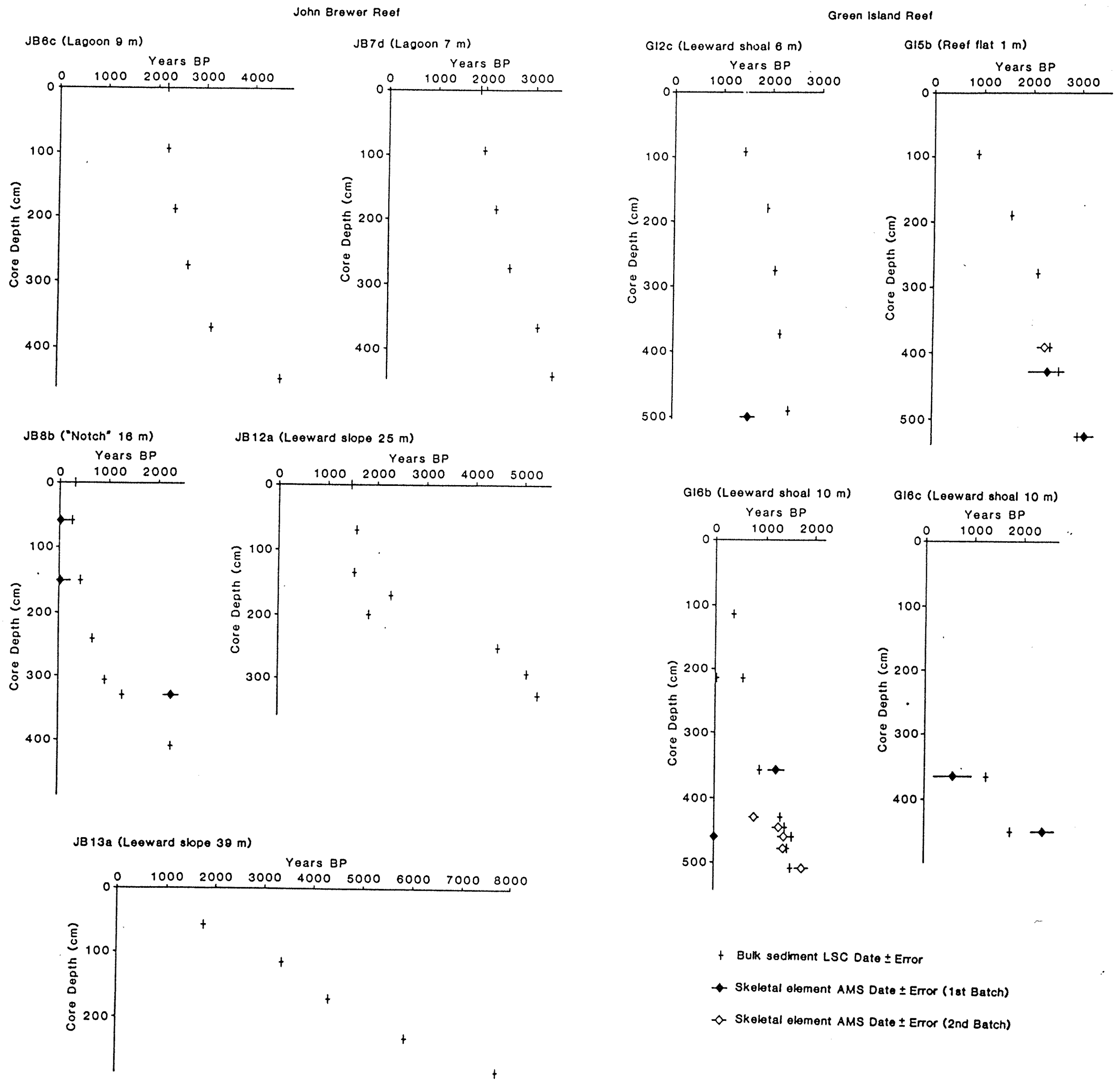

John Brewer Reef
TN
Leeward slope
(JB39)
Lagoon
Reef flat
(JB58)
Windward slope
Western slope
0 1 km
14 3 4 1 4 18 3 3 4 2 1 7 8 1 1 1 1 16 1 3 1 5 4 1 1 2 1 4 19 12 88 93 41 71 46 8 72 43 11 6 6 2 1 2
Green Island Reef
TN
Leeward shoal
Cay
Reef flat
(GI34)
Windward shoal
South-west slope
(GI31)
0 1 km
17 29 7 15 12 11 11 27 13 46 4 18 5 23 6 38 1 23 3 5 18 20 2 18 133 39 3 1 2 64 16 51 20 39 18 13 29 22 69 12 18 49 26
Heron Island Reef
TN
Leeward slope
Leeward shoal
Western shoal
Cay
1
Reef flat
Blue lagoon
Shallow lagoon
Channel
1
Wistari Reef
Inter-reef shoal
Windward slope
0 1 km


John Brewer Reef
TN
Leeward slope
"Notch"
8
13
11
12
1
Lagoon
6
7
0
1 km


Green Island Reef
TN
Leeward shoal
1
2
3
4
5
6
Reef flat
0
1 km


Lagoon 8 m
JB1a
JB1c
Lagoon 9 m
JB6a
JB6c
2180 ± 90
2190 ± 90
2340 ± 90
2620 ± 90
3210 ± 90
4530 ± 90
Lagoon 7 m
JB7c
JB7d
1870 ± 90
1940 ± 90
2200 ± 90
2480 ± 90
3080 ± 90
3390 ± 90
"Notch" 16 m
JB8a
JB8b
310 ± 80
250 ± 70
410 ± 70
680 ± 70
970 ± 80
1330 ± 70
2310 ± 80
Core Depth (cm)
0
100
200
300
400
500
0 5
0 5 10
Leeward slope 33 m
JB11c
JB11d
JB11e
JB11f
Leeward slope 25 m
JB12a
JB12b
JB12c
1480 ± 90
1590 ± 80
1550 ± 80
2320 ± 90
1860 ± 80
4500 ± 90
5080 ± 100
5320 ± 90
Leeward slope 39 m
JB13a
JB13b
1770 ± 80
3390 ± 90
4340 ± 90
5880 ± 90
7740 ± 100
LSC-Dated Sample
AMS-Dated Sample


Reef flat 3 m
Leeward shoal 6 m
Leeward shoal 7 m
GI1b
GI1c
GI2b
GI2c
GI3a
GI3b
Core Depth (cm)
0
100
200
300
400
500
1410 ± 80
1880 ± 80
2060 ± 80
2170 ± 80
2350 ± 80
0 5 10
0 5
Leeward shoal 11 m
Reef flat 1 m
Leeward shoal 10 m
GI4a
GI4d
GI5b
GI5c
GI6b
GI6c
880 ± 80
1580 ± 80
2120 ± 80
2380 ± 80
2550 ± 80
2960 ± 80
370 ± 80
40 ± 70
580 ± 80
930 ± 80
1370 ± 80
1460 ± 80
1580 ± 80
1500 ± 80
1550 ± 70
1270 ± 80
1760 ± 80
0 5 10 15
LSC-Dated Sample
AMS-Dated Sample

John Brewer Reef
Green Island Reef
JB6c (Lagoon 9 m)
JB7d (Lagoon 7 m)
GI2c (Leeward shoal 6 m)
GI5b (Reef flat 1 m)
JB8b ("Notch" 16 m)
JB12a (Leeward slope 25 m)
GI6b (Leeward shoal 10 m)
GI6c (Leeward shoal 10 m)
JB13a (Leeward slope 39 m)
Years BP
Core Depth (cm)
0
1000
2000
3000
4000
5000
6000
7000
8000
100
200
300
400
500
+ Bulk sediment LSC Date ± Error
◆ Skeletal element AMS Date ± Error (1st Batch)
◇ Skeletal element AMS Date ± Error (2nd Batch)